

A living *Tesseropora* (Cirripedia; Balanomorpha) from Bermuda and the Azores; first records from the Atlantic since the Oligocene

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ABSTRACT.—*Tesseropora* occupies a central position in the evolution of the Tetracitinae, and likely the Tetracitellinae, by virtue of geological age and comparative morphology. Considering the biogeography of the two extant species from the Indo-West Pacific, the genus is apparently favored by the special requirements related to perpetuation of insular populations. The more highly evolved genus *Tetracitella*, on the other hand, is for the most part prevalent on continental shores where the opportunities for competitive interactions are greater. Recognition of a new species of *Tesseropora* from Bermuda and the Azores corroborates the primarily insular nature of the genus and enhances the concept that oceanic islands can act as refugia for ancient forms.

In consideration of the special adaptations needed by marine organisms to perpetuate their populations on oceanic islands on one hand, and the isolation, ephemerality, short faunal lists and concomitant unbalanced biotas of oceanic islands on the other, one would expect vagile, eurytopic taxa, or the descendants thereof, to be disproportionately prevalent on them. Many such taxa are early members of lineages having advanced members more commonly found in centers of distribution frequently contiguous with continental shores, and this is apparently the basis for the concept that insular situations can act as refugia for ancient forms.

Tesseropora isseli (de Alessandri, 1895: 296), from the Oligocene of Italy, is the oldest known tetracitid. Pilsbry (1916: 259), when reflecting on the significance of the single row of parietal tubes in the wall of the only extant species of the genus known at the time, remarked “. . . [*T. rosea* (Krauss, 1848)] is to be regarded as an unprogressive form, which retains characters of the ancestral stock of the genus, elsewhere found [in the Tetracitidae] only in an early stage of development”, a fact noted earlier by Darwin (1854:336). Since Pilsbry, *Tesseropora* has maintained a more or less central position in considerations of the evolution of the tetracitine and tetracitelline branches of the family (Zullo, 1968:274; Ross, 1969:239; Newman and Ross, 1976:47).

From a biogeographic point of view, *Tesseropora* as previously known would be considered primarily an insular Indo-Pacific genus; *T. rosea* occurring solely in the southern hemisphere from the southern tip of South Africa to southern Australia, the Kermadec Islands and New Caledonia, and *T. wireni* (Nilsson-Cantell, 1921: 366) for the most part in the northern hemisphere, from Dar-es-Salaam east, from Chagos Bank to Wake and perhaps the Hawaiian Islands. The counterpart of *Tesseropora* on continental shores is the more advanced genus *Tetracitella*. Recognition of an Atlantic *Tesseropora*, on Bermuda and the Azores, is therefore of considerable significance not only in extending the modern distribution of the genus, but also in corroborating biogeographical inferences that oceanic islands can act as refugia for ancient forms (see Fig. 4).

Superfamily Coronuloidea Leach, 1825¹
 Family Tetracelitidae Gruvel, 1903
 Subfamily Tetracelitinae Gruvel, 1903
Tesseropora Pilsbry, 1916
Tesseropora atlantica n. sp.

Tetracelita porosa: Verrill, 1901:22 (Bermuda).

Tetracelita squamosa stalactifera: Henry, 1958:224 (Bermuda); Ross, 1962:33; Werner, 1967:70; Ross, 1968:8.

Tetracelita squamosa var. *elegans*: Baker, 1967: 46 (Azores).

Diagnosis.—A small (diameter of largest spec. approx. 10mm), white *Tesseropora* with moderately developed radii having eroded and (or) oblique summits concomitant with a somewhat flaring, toothed orifice; scutal adductor ridge in line and nearly continuous with articular ridge; intermediate articles of cirrus VI supporting five pairs of setae; crest of labrum lacking obvious teeth.

Description.—Shell white or with a slight pinkish cast; conical; radii and alae moderately well developed with summits parallel to base; commonly, when eroded, orifice moderately toothed (Fig. 1). Surface of solid radii marked by transverse ridges, and of paries by low longitudinal ribs equal to the number of longitudinal tubes in the wall. Sheath white, adpressed, continuous with interior surface of paries; region below sheath smooth or marked by reminiscences of small basal denticles in the form of numerous fine ribs. Longitudinal septa normal to inner and outer laminae, forming a single row of irregular tubes (Fig. 2d); one or more incomplete septa may be present on inner surface of outer lamina. None of the specimens available is sufficiently eroded to expose the secondary filling of the parietal tubes, but grinding revealed a white filling near the apex. No calcareous spines extend from the inner surface of the outer lamina into the parietal tubes as reported for *wireni* by Henry (1957: 33), and as we have observed in *rosea*, but older and larger specimens might have them. Basis calcareous, solid, thick, adhering strongly to the wall. Opercular valves white. Scutum with well defined adductor muscle pit and ridge, the curvature of the latter being virtually continuous with that of the articular ridge (Fig. 2b); rostral and lateral depressor muscle crests well defined in larger specimens, apparently increasing in number with age; rostral depressors essentially lacking in small specimens. Tergum with material forming beak undifferentiated from rest of valve and readily broken or worn away; spur furrow open, broad and shallow.

Trophi undistinguished except for the lack of conspicuous teeth on the labrum (Fig. 3g). Cirral counts for two specimens from Bermuda follow:

	I	II	III	IV	V	VI
	$\frac{12}{6}$	$\frac{8}{9}$	$\frac{7}{10}$	$\frac{14}{16}$	$\frac{16}{18}$	$\frac{17}{18}$
Specimen 1						
	$\frac{12}{8}$	$\frac{8}{8}$	$\frac{8}{9}$	$\frac{14}{14}$	$\frac{16}{18}$	$\frac{16}{17}$
	$\frac{11}{6}$	$\frac{6}{7}$	$\frac{7}{7}$	$\frac{12}{16}$	$\frac{16}{17}$	$\frac{16}{xx}$
Specimen 2						
	$\frac{12}{6}$	$\frac{6}{7}$	$\frac{7}{9}$	$\frac{12}{14}$	$\frac{15}{17}$	$\frac{18}{19}$

¹Due to an oversight on our part the superfamilial name Balanomorphoidea must be suppressed in favor of Coronuloidea (see Newman and Ross, in press).



Figure 1. *Tesseropora atlantica* n. sp., on an oyster from Argus Tower, Bermuda.

The third cirrus is normal in form (rami not antenniform); supporting three types of bipectinate setae (Fig. 3c-e), the heaviest (card) being rarely observed; surfaces of the lesser curvature armed with short, curved spines or denticles (Fig. 3f). Intermediate articles of cirrus VI bearing five pairs of setae with occasional pairs or small clusters of short bristles between major pairs (Fig. 3b). The intromittant organ is normal.

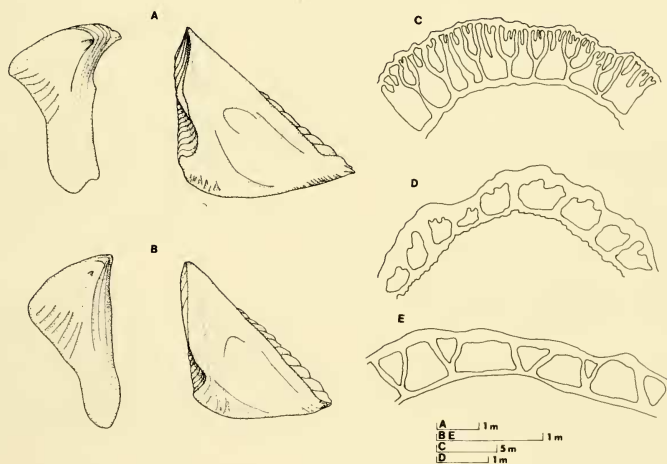


Figure 2. A, Right tergum and scutum of *Tesseropora wireni* (Nilsson-Cantell) from Wake Island (type locality of *T. w. pacifica*, approx. 20mm basal diam.); and B, of *T. atlantica* n. sp. from Bermuda (type, approx. 11mm diam.); C, D, and E, basal margins of parietes of *T. wireni*, *T. atlantica* and very young *Tetracrita stalactifera* (Lamarck), respectively.

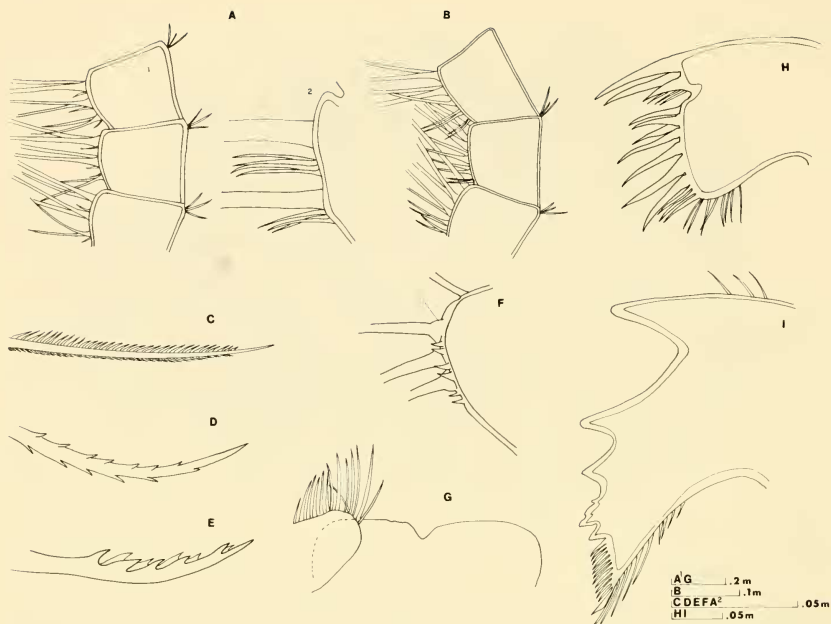


Figure 3. A¹, intermediate articles of sixth cirrus in *Tesseropora wireni* (approx. 20mm diam.) and A², portion of an intermediate article of the sixth cirrus in *T. wireni* (approx. 40mm diam.) from Wake I., the latter showing the increase in number of small spines below each of the larger two pairs of setae. B-I *Tesseropora atlantica* n. sp.: B, intermediate articles of sixth cirrus; C, D, and E, specialized setae; F, spines found on the third cirrus; G, labrum (right palp deleted); H, first maxilla, I, mandible.

Type material.—Gurnet Rock, Bermuda (type locality), intertidal with *Chthamalus* and *Catophragmus* (see Henry, 1958); USNM cat. no. 168472 (holotype); BM(NH) 1976.1281 (paratype) [USNM cat. no. 102827 (type lot; USNM acc. no. 195758)]. Argus Tower, southwest of Bermuda, subtidal (2-3m), dried, on an oyster (cf. *Lopha frons*), W. Sterrer coll., April, 1976, BM(NH) 1976.1282, USNM cat. no. 168473. Urzelina, São Jorge, Azores, subtidal, Chelsea College Azores Expedition (see Baker, 1967), A. J. Southward leg., BM(NH) 1976.1283.

Reference material.—One often must rely on published descriptions in making judgements on the distinctiveness of a species. By good fortune *Tesseropora* is a small genus, and we had comparative materials in our collections of the other species upon which to base our analysis.

Tesseropora wireni (Nilsson-Cantell):

Wake Island [type locality of *T. w. pacifica* (Pilsbry)], numerous large specimens with *Euraphia intertexta* (Darwin), 1854, R. McFarlan coll., 27 Dec. 1964.

Ulupau, Hawaii, numerous small specimens from 6" pipe of seawater system, B. L. Burch leg., 28 Sept. 1976 (not *T. wireni* s. s., see discussion below).

South Field Beach, Moen Island, Truk, Caroline Islands, a single small specimen from the underside of an intertidal coral boulder resting on sand, W. A. Newman coll., June, 1956.

Dublon Channel, Truk, Caroline Islands, numerous small specimens on dead coral from underside of buoy, W. A. Newman coll., June, 1956 (see Newman, 1960, pl. 20, fig. 1).

Table 1. Distinguishing characteristics of extant species of *Tesseropora*.

Species	Form and size	Color: 1-wall 2-shield 3-filling 4-valves	Radii	Parietal tubes	Scutum	Labrum	Cirrus III	Intermediate segments Cirrus VI
<i>atlantica</i>	Steeply conical when young; ? when old; approx. 10 mm in basal diameter	1-white 2-white 3-white 4-white	moderately wide	in single row	adductor ridge in line with articular ridge	apparently without conspicuous teeth	occasionally armed with heavy bipecti- nate setae (cards)	five pairs of setae per article
<i>rosea</i>	Steeply conical; up to 30mm	1-white 2-dirty white tinted pink 3-usually pink 4-white	ditto	ditto	adductor ridge overlapping articular ridge	with several teeth on each side of shallow notch	armed with numerous cards	three pairs of setae per article, num- erous short setae in dense bunches below two major prs.
<i>wireni</i>	Steeply conical when young; low when old; up to 40mm	1-white 2-usually dark red- brown 3-usually pink 4-white	extremely narrow to lacking	divided into sec- ondary and tertiary rows bas- ally	ditto	ditto	armed with bipinnate but not bipectinate setae (cards)	as <i>rosea</i> but with a few short setae in groups below two major pairs

Kwajalein Atoll, Marshall Islands, Carmarsel Expedition (CRS-325), intertidal, on iron piling, numerous specimens with *E. intertexta*, W. A. Newman coll., 2 April 1967.

Ulul Island, Namonuito Atoll, Caroline Islands, Carmarsel Expedition (CRS-307), several specimens in *Heliopora*, with *Lithoglyptes wilsoni* Tomlinson, 1969, 10m, W. A. Newman coll., 15 Feb. 1967.

Port of Palau, Arakabesan Passage near Periryu Island, Caroline Islands, in *Heliopora*, Seto Marine Biological Laboratory no. 81, F. Hiro coll., 1934 (see Hiro, 1935: 5; the collection studied consists of some fragments of *Tesseropora*, and several complete specimens of a pyrgomatid imbedded in the coral).

Tesseropora rosea (Krauss):

Gerroa (south of Port Kembla), New South Wales, Australia, on mid-tidal rocks, E. Pope coll., 2 April 1963.

Bouvail-Baie des Tortues, New Caledonia, a single large specimen, dried, from a rock, J. C. Plaziat coll., 5 Nov. 1973.

DISCUSSION

Only one species referable to *Tesseropora* (*Conia rosea* Krauss) was known when Darwin (1854) published his incomparable monograph on the sessile barnacles. The second, *T. isseli* (de Alessandri, 1895), from the Oligocene of Italy, while morphologically close to *rosea*, is known only by the wall and need not concern us here. A third species, *wireni*, was described by Nilsson-Cantell (1921: 366), followed by *wireni pacifica* (Pilsbry, 1928: 312) and *wireni africana* (Nilsson-Cantell, 1932: 14). Henry (1957: 33) elevated *pacifica* to specific rank. We believe, as Zullo (1968) seemingly did, that there is presently insufficient data to distinguish *pacifica* from *wireni* at the specific or the subspecific level, and believe the same is true of *africana*. Therefore, we tentatively treat living *Tesseropora* as containing but two taxa, *rosea* and *wireni*.

The new species, *T. atlantica*, can be distinguished from both *rosea* and *wireni* by a number of characters (Table 1), the most obvious being the alignment of the scutal adductor ridge with the articular ridge rather than passing well inward of it (compare Figs. 2b and 2a), and the intermediate segments of cirrus VI bearing five rather than three pairs of setae (compare Figs. 3b and 3a). *Tesseropora rosea*, known from New South Wales, South Africa and New Caledonia, differs from mature *wireni* in retaining a single row of parietal tubes throughout life. While secondary riblets develop on the interior of the outer lamina, as noted by

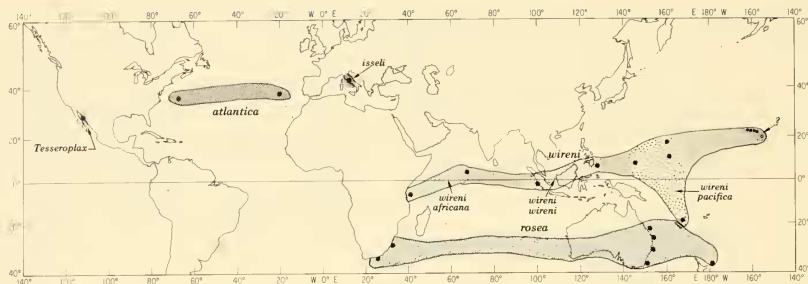


Figure 4. Distribution of *Tesseropora* spp. and the closely related *Tesseroplax unisemita* (Zullo, 1968). The latter is known only from Pliocene sediments in the Gulf of California (cf. Ross, 1969). The other significant fossil record is that for *Tesseropora isseli* from the Oligocene of Italy. The Indo-West Pacific species, *T. rosea* and *T. wireni*, while morphologically distinct, are more closely related to each other than to *T. atlantica* from Bermuda and the Azores. At the present level of our knowledge the taxonomic status of the so-called subspecies of *T. wireni* cannot be sustained. The assignment of the Hawaiian form to *T. wireni* is questioned herein.

Darwin (1854: 336), they are normal to the surface and thereby fail to join the primary septa to form secondary tubes. Young *wireni*, and it is young specimens that are apparently most commonly collected and described, also have a single row of essentially square parietal tubes, but with growth the longitudinal septa join some of the riblets on the interior of the outer lamina, singly or in pairs, leading to the dendritic pattern of the septa separating the secondary tubes formed in the process. (Fig. 2c). Although we have not observed secondary tubes in *atlantica*, Henry (1958: 224) noted a few in the rostrum of the largest specimen she examined. The appearance of large, eroded *atlantica* may appear more like that of *wireni* than that of *rosea*.

Young, uneroded *rosea* were described by Darwin (1854: 323), and apparently the best character that might be used to distinguish them from young *wireni* would be moderate to well developed radii in the former. It follows that young uneroded *rosea* cannot be distinguished from *atlantica*, at the present state of our knowledge, since both have radii. The only characters presently known that will separate them are the interiors of the scuta, the pinkish rather than white filling of the parietal tubes, and the nature of the cirri described above.

The specimens of *Tesseropora* from Hawaii are not typical of *wireni*. All available are small, less than 3 mm in basal diameter, and therefore they had not likely completed their development. Nonetheless, several contained larvae and were therefore at least sexually mature (see discussion of larvae below). This Hawaiian material is similar to the *wireni* studied from elsewhere in having much reduced radii and in having a toothed labrum, but the adductor ridge of the scutum is closer to being in line with the articular ridge (similar to *atlantica*), the sheath is white (Pilsbry, 1928: 313, noted that the sheath of *wireni* ranges from prussian blue to white, but his material included specimens from Necker Island in the Hawaiian Archipelago as well as from Wake Island), the cirral counts are lower, cirrus III has bipectinate (cards) as well as bipinnate setae, and the intermediate segments of cirrus VI bear three, four or five pairs of setae (on the same ramus), but commonly four, a number intermediate between that found in *atlantica*, and *wireni* and *rosea*. The differences noted here make it difficult to assign this material to *wireni* for, if consistent, they would be sufficient to allow one to propose the Hawaiian form as a new species. However, such a decision will have to await further study.

Both *rosea* and *wireni* can attain basal diameters approaching 40 mm, and in most large specimens the outer lamina of the shell is all but completely eroded, exposing the generally pinkish, more resistant material lining the interior of the parietal tubes. In a specimen of *rosea* from New Caledonia most of these run continuously from the apex to the base, but a few can be observed on the exterior, beginning more than halfway down the wall rather than at the apex, and this indicates, although there is predominantly a single row of tubes in the wall, a few supernumerary ones occasionally develop. Zullo (1968: 272) noted comparable development in this species from southeast Australia. In appearance, *wireni* is comparable, but many more of the pillars exposed by erosion, other than the primary ones, begin at varying distances down the shell below the apex. Thus, the general ribbing appears finer because of the more numerous development of secondary parietal tubes. None of the specimens of *atlantica* is sufficiently eroded to expose the pillars.

It is perhaps significant that *wireni*, although ranging from East Africa to Wake Island and perhaps to Hawaii, appears to be a relatively rare species. Also, most of the material described has been of relatively young uneroded specimens, up to but generally smaller than 15 mm or so in diameter. One is led to suspect the same thing may be true for *atlantica* — the specimens on hand are relatively young individuals and the species is likely not confined solely to Bermuda and the Azores.

Verrill (1901: 22) identified a Bermudan form as *Tetraclita porosa* (= *squamosa*). Although we cannot prove he had *Tesseropora* rather than *Tetraclita* s. s., it does seem highly likely because he stated, "This is the common, small, sessile barnacle found on the rocks between tides, with the general appearance of some species of *Balanus*". Species of *Tetraclita*, however, are generally relatively large, and it is the erosion of the outer lamina of the shell, exposing the colored infilling of the parietal tubes, that gives them the characteristic tetraclitid appearance. On the other hand, *atlantica* is known as a small species, and in being uneroded it does have a somewhat balanid appearance. In any event, his identification apparently led Henry (1958: 224) to consider the Stephenson's material to be *T. squamosa stalactifera*, the only "subspecies" of the *squamosa* complex known from the Caribbean. The single row of tubes in the wall did not invalidate this conclusion for, as Darwin (1854: 323) noted, in very young specimens of *Tetraclita* there is only a single row of tubes (Fig. 2e). During growth, these are added to by bifurcation of the septa at the outer lamina very early in *Tetraclita* and *Tetraclitella*, quite a little later in *wireni* and possibly *atlantica*, and hardly at all in *rosea*. It is important to note that in *Tetraclita* the septa forming the single row of tubes are at angles other than normal to the inner lamina, but in *Tesseropora* they are normal or essentially normal (compare Figs. 2c and 2d with 2e). This and the presence of a calcareous basis in the latter serves to distinguish the two genera.

The development of radii, a tubiferous wall and a strong calcareous basis would appear to be fundamental to the Tetraclitidae, all three being the principal advances in the shell made over the bathylasmatid (ancestral) level of organization (Newman and Ross, 1976: 20). Radii greatly strengthen the wall, important in the surf zone (Darwin, 1854: 56; Barnes, Read and Topinka, 1970: 82). A tubiferous wall, especially when secondarily filled, places an additional barrier to erosion and boring organisms (Ross, 1970: 9; Newman and Ross, 1971: 159). A calcareous basis conveys an advantage in forming a strong attachment (Newman, Zullo and Wainwright, 1967: 170) and in retarding desiccation in intertidal forms, especially in the tropics where porous reef limestones are common (Southward and Newman, in press). *Tesseropora* has these advanced features. But the most successful

tetraclitid today, in terms of being an abundant intertidal dominant, is *Tetraclita*. The genus has carried the filled tubiferous wall to the extreme, and perhaps the great thickness achieved has allowed it to give up radii, but why it has also given up a calcareous basis is an enigma, unless it has gained a degree of limited motility, as was demonstrated for *Semibalanus balanoides* by Crisp (1960: 1208).

Tetraclitella divisa, also primarily an insular species, is known to carry embryonic development through to the cyprid stage, passing the naupliar stages in the egg (Nilsson-Cantell, 1921: 93, 364; Ross, 1961: 211). Cyprid larvae are incapable of feeding and, because they also are not known to remain long in the plankton, they are not likely propagules for long-range dispersal (Newman and Tomlinson, 1974: 208). The direct production of the non-feeding stage in *divisa* could be an adaptation to the relatively sterile waters of most oceanic situations, but because most balanomorphans of such regions apparently have nauplii, this could be only part of the reason, another being the selection for mechanisms that favor maintaining populations on isolated oceanic islands too distant to be regularly reached from elsewhere by ordinary means. Species having a tendency to suppress the nauplius would thereby be likely candidates for maintaining populations on isolated insular situations. It is interesting therefore to note that the larvae of *Tesseropora* from Hawaii just mentioned are released as cyprids, and it will be interesting to see if the life histories of other populations or species of the genus are so modified.

Although the suppression of the nauplius may aid in maintaining isolated insular populations, such populations would appear to have removed themselves from the list of potential island colonizers by larval propagules. Furthermore, because islands are ephemeral in terms of geological time relative to continental shores, the time to extinction of such lineages would be substantially shortened. However, this problem can and apparently has been circumvented because some sedentary species with short range larvae have achieved and apparently maintain distributions over great expanses of open water. So far as *divisa* is concerned, and the likewise virtually cosmopolitan *Balanus trigonus*, transport of adult propagules by rafting, but more so by other organisms, seems likely. One of us (W.A.N.) has found adults of the former washed ashore on Majuro Atoll in the Marshall Islands attached to the shell of the pelagic barnacle *Lepas*, and of the latter, attached to the shell of the whale barnacle *Coronula*. These species therefore have the potential of being transported great distances as adults, and this may explain their virtually cosmopolitan distributions in the warm seas of the world.

No tetraclitid is known to form an obligate commensal relationship, although individuals of some species are found on other organisms, the most notable being *wireni*, which occurs embedded in the blue coral *Heliopora*. If the history of the genus continues and it is eventually completely replaced as a free-living form, conceivably *wireni* could persist as an obligate commensal.

ACKNOWLEDGMENTS

We thank Alan J. Southward, Marine Biological Association of the United Kingdom, for bringing this problem to our attention and for providing specimens from Bermuda and the Azores. We would also like to thank T. E. Bowman, National Museum of Natural History, William K. Emerson, American Museum of Natural History, W. D. Hartman, Yale Peabody Museum and W. E. Sterrer, Bermuda Biological Station for their attempts to locate voucher specimens from Bermuda collected either by Verrill or others near the turn of the century; and G. A. Boxshall, British Museum (Natural History) for attempts to locate material from the Azores. Thanks are also due Huzio Utinomi, who kindly arranged for the loan of specimens from the Seto Marine Biological Laboratory, Beatrice L. Burch for the somewhat enigmatic specimens from Hawaii, and Gayle Kidder for technical assistance and preparation of the figures. Work supported, in part, by the National Science Foundation (DEB-7517149).

REFERENCES

- Baker, I. H., 1967. Cirripedia in, Chelsea College Azores Expedition, 1965. Final Report: 46-47. University of London.
- Barnard, K. H., 1924. Contributions to the crustacean fauna of South Africa. No. 7. Cirripedia. Annals South African Museum 20: 1-103.
- Barnes, H., R. Read and J. Topinka, 1970. The behaviour on impactation by solids of some common cirripedes and relation to their normal habitat. Journal of Experimental Marine Biology and Ecology 5(1): 70-87.
- Crisp, D. J., 1960. Mobility of barnacles. Nature 188(4757): 1208-1209.
- Darwin, C., 1854. A Monograph on the subclass Cirripedia with figures of all the species. The Balanidae, the Verrucidae, etc. Ray Society, London, 684pp.
- de Alessandri, G., 1895. Contribuzione allo studio dei Cirripedi fossili d'Italia. Societa Geologica Italiana, Bollettino 13(3): 234-314.
- Edmondson, C. H., 1946. Reef and shore fauna of Hawaii. Bernice P. Bishop Museum Special Publication 22. 381pp.
- Endean, R., W. Stephenson and R. Kenny, 1956. The ecology and distribution of intertidal organisms on certain islands off the Queensland coast. Australian Journal of Marine and Freshwater Research 7(3): 317-342.
- Foster, B. A., 1974. The barnacles of Fiji, with observations on the ecology of barnacles on tropical shores. Pacific Science 28(1): 35-56.
- Henry, D. P., 1957. Some littoral barnacles from the Tuamotu, Marshall, and Caroline Islands. Proceedings U.S. National Museum 107(3381): 25-38.
- Henry, D. P., 1958. Intertidal barnacles of Bermuda. Journal of Marine Research 17: 215-234.
- Hiro, F., 1936. On the commensalism between the cirripeds and other animals. Ecological Review, Sendai 2(1): 58-65.
- Hiro, F., 1937. Cirripeds of the Palao Islands. Palao Tropical Biological Station Studies 1: 37-72.
- Krauss, F., 1848. Die sudafrikanischen Mollusken. Ein Beitrag zur Kenntniss der Mollusken des Kap- und Natal-landes und zur geographischen Verbreitung derselben, mit Beschreibung und Abbildung der neuen Arten. Stuttgart.
- Macnae, W. and M. Kalk (eds.), 1969. A natural history of Inhaca Islands, Mozambique. Witwatersrand University Press, Johannesburg, South Africa. 163pp.
- Matsuda, C., 1973. A shoreline survey of free-living intertidal barnacles on the island of Oahu, Hawaii. 60pp. Unpublished master's thesis, Dept. of Zoology, University of Hawaii.
- Newman, W. A., 1960. The paucity of intertidal barnacles in the Tropical Western Pacific. Veliger 2(4): 89-94.
- Newman, W. A. and A. Ross, 1971. Antarctic Cirripedia. Antarctic Research Series 14. 257 pp. American Geophysical Union.
- Newman, W. A. and A. Ross, 1976. Revision of the balanomorph barnacles; including a catalog of the species. San Diego Society of Natural History, Memoir 9. 108pp.
- Newman, W. A. and A. Ross, in press. Superfamilies of the Balanomorphs. Crustaceana.
- Newman, W. A. and J. T. Tomlinson, 1974. Ontogenetic dimorphism in *Lithoglyptes* (Cirripedia: Acrothoracica). Crustaceana 27(2): 204-208.
- Newman, W. A., V. A. Zullo and W. A. Wainwright, 1967. A critique on recent concepts of growth in Balanomorphs (Cirripedia, Thoracica). Crustaceana 12(2): 167-178.
- Nilsson-Cantell, C. A., 1921. Cirripeden-Studien. Zur Kenntnis der Biologie, Anatomie und Systematik dieser Gruppe. Zoologiska Bidrag Uppsala 7:75-395.
- Nilsson-Cantell, C. A., 1932. Neue Balaniden aus Sud- und Ost-Afrika in dem Berliner Museum. Arkiv fur Zoologi 24A(6):1-18.
- Pilsbry, H. A., 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. Bulletin of the U.S. National Museum 93:1-366.
- Pilsbry, H. A., 1928. Littoral barnacles of the Hawaiian Islands and Japan. Proceedings Academy Natural Sciences Philadelphia 79: 305-317.
- Pope, E., 1945. A simplified key to the sessile barnacles found on the rocks, boats, wharf piles and other installations in Port Jackson and adjacent waters. Records of the Australian Museum 21(6): 351-372.
- Ross, A., 1961. A new cirriped from the Hawaiian Islands. Crustaceana, 2(3): 209-212.
- Ross, A., 1962. Results of the Puritan-American Museum of Natural History Expedition to western Mexico. No. 15. The littoral balanomorph Cirripedia. American Museum Novitates 2084: 1-44.
- Ross, A., 1968. Bredin-Archbold-Smithsonian Biological Survey of Dominica. 8. The intertidal balanomorph Cirripedia. Proceedings U.S. National Museum 125 (3663): 1-22.
- Ross, A., 1969. Studies on the Tetracitidae (Cirripedia: Thoracica): Revision of *Tetracitita*. Transactions San Diego Society of Natural History 15(15):

- 237-251.
- Ross, A., 1970. Studies on the Tetracitidae (Cirripedia: Thoracica): A proposed new genus for the austral species *Tetracitella purpurascens breviscutum*. Transactions San Diego Society of Natural History 16(1): 1-12.
- Smith, W. A., 1971. Crustacea: Cirripedes from Diego Garcia. Atoll Research Bulletin 149:103.
- Southward, A. J. and W. A. Newman, in press. Aspects of the ecology and biogeography of the intertidal and shallow-water balanomorph Cirripedia of the Caribbean and adjacent sea-areas. CICAR-II Symposium, Caracas, Venezuela, July 12-16, 1976.
- Verrill, A. E., 1901. Additions to the fauna of the Bermudas from the Yale Expedition of 1901, with notes on other species. Transactions Connecticut Academy of Arts and Sciences 11(1): 15-62.
- Werner, W. E., 1967. The distribution and ecology of the barnacle *Balanus trigonus*. Bulletin of Marine Science 17(1): 64-84.
- Zullo, V. A., 1968. *Tesseropora* Pilsbry (Cirripedia, Thoracica) from the Pliocene of the Gulf of California. Crustaceana 15(3): 272-274.

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Contribution No. 692 from the Bermuda Biological Station for Research, Inc.

Contribution of the Scripps Institution of Oceanography, new series.